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## **The Evolution of Body Size: What Keeps Organisms Small?**

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# THE QUARTERLY REVIEW of BIOLOGY



## THE EVOLUTION OF BODY SIZE: WHAT KEEPS ORGANISMS SMALL?

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### ABSTRACT

*It is widely agreed that fecundity selection and sexual selection are the major evolutionary forces that select for larger body size in most organisms. The general, equilibrium view is that selection for large body size is eventually counterbalanced by opposing selective forces. While the evidence for selection favoring larger body size is overwhelming, counterbalancing selection favoring small body size is often masked by the good condition of the larger organism and is therefore less obvious. The suggested costs of large size are: (1) viability costs in juveniles due to long development and/or fast growth; (2) viability costs in adults and juveniles due to predation, parasitism, or starvation because of reduced agility, increased detectability, higher energy requirements, heat stress, and/or intrinsic costs of reproduction; (3) decreased mating success of large males due to reduced agility and/or high energy requirements; and (4) decreased reproductive success of large females and males due to late reproduction. A review of the literature indicates a substantial lack of empirical evidence for these various mechanisms and highlights the need for experimental studies that specifically address the fitness costs of being large at the ecological, physiological, and genetic levels. Specifically, theoretical investigations and comprehensive case studies of particular model species are needed to elucidate whether sporadic selection in time and space is sufficient to counterbalance perpetual and strong selection for large body size.*

### INTRODUCTION

**B**ODY SIZE continues to be one of the most important quantitative traits under evolutionary scrutiny. This is because body size is strongly correlated with many physiological and fitness characters (Peters 1983; Reiss 1989; Roff 1992; Stearns 1992). Body size also exhibits prominent general evolutionary trends. Taxa are believed to evolve larger body

sizes over evolutionary time (Cope's rule: Bonner 1988; McLain 1993; Jablonski 1997), and sexual size dimorphism (SSD) increases with size when males are the larger sex but decreases with size when females are the larger sex (Rensch's rule: Rensch 1959; Fairbairn 1997).

It is widely agreed that fecundity selection in females and sexual selection in males are the major evolutionary forces that select for

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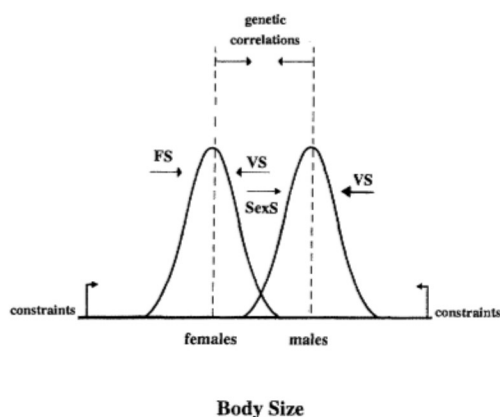


FIGURE 1. MAJOR SELECTIVE PRESSURES THAT AFFECT THE EVOLUTION OF BODY SIZE AND SEXUAL SIZE DIMORPHISM (SSD).

Body size distributions for the case where males are larger than females are depicted. Fecundity selection (FS) tends to select for increased body size in females, and sexual selection (SexS) for increased body size in males; adult and juvenile viability selection (VS) is assumed to select for smaller body size in both sexes. These three major selective pressures are thought to equilibrate differentially in the sexes, resulting in the SSD observed in any particular species. Some general constraints as well as genetic correlations between the sexes that potentially limit the evolution of SSD are indicated.

larger body size in many organisms (Figure 1). In most ectotherms, the number of eggs a female produces increases strongly with body size (Wootton 1979; Shine 1988, 1989; Honek 1993; Andersson 1994:252). Even in endotherms, where female reproductive success is often not limited by propagule number, larger females often produce offspring of better quality (Clutton-Brock et al. 1982, 1988). There is also ample empirical evidence in many species for greater mating and reproductive success of large males, be it mediated by male-male competition or female choice (Shine 1989; Andersson 1994). The general, equilibrium view is that selection for large body size is eventually counterbalanced by opposing selective forces, primarily viability selection (Endler 1986; Arak 1988; Travis 1989; Schluter et al. 1991; Andersson 1994; Figure 1). Such counterbalancing selection may be sufficient if it oc-

curs in only one sex, because body size is typically highly genetically correlated between the sexes (Lande 1980; Reeve and Fairbairn 1996). Within some limits set by genetic (Reeve and Fairbairn 1996), phylogenetic (Cheverud et al. 1985), and developmental and physiological (Peters 1983; Reiss 1989) constraints, the three major selective pressures are thus thought to equilibrate differentially in the sexes, resulting in the SSD observed in a particular species (Fairbairn 1997; Figure 1). However, while the evidence for fecundity and sexual selection favoring larger body size is overwhelming, evidence for viability or any other form of selection favoring small body size is relatively scant.

This article outlines the mechanisms proposed in the literature that are believed to limit body size in multicellular organisms (Table 1). The arguments can be subdivided into three classes according to the level of biological organization at which they are expressed: ecological, evolutionary, and physiological. I comprehensively review and discuss the evidence for these mechanisms in an attempt to understand why demonstrations of the disadvantages of large body size are relatively uncommon in the literature, even though they are crucial for explaining why we are not surrounded by gigantic organisms. Studies (up to 1998) in the literature that demonstrate the disadvantages of any morphological trait indicative of large body size were compiled. The studies are of varying quality, but no restrictions were placed on the findings; final judgement is left to the reader. The vast majority of studies were on animals, but studies on plants were included whenever available.

#### ECOLOGICAL MECHANISMS

##### VIABILITY DISADVANTAGES OF LARGE BODY SIZE

Viability selection against large body size can occur at the preadult (juvenile) and/or the adult life stages. Juvenile mortality rates feature centrally in most life-history optimality models that try to predict optimal growth, development, age, and size at maturity (Roff 1980, 1992; Stearns and Koella 1986; Kozłowski 1992; Stearns 1992). These are the viability costs of **becoming** large.

There are two distinct sources of mortality that relate to the body size eventually achieved



TABLE 1  
*Mechanisms that select against large body size together with associated costs of being large*

| Selection mechanism   | Cost of large size   |
|---|--|
| 1. Larval or adult viability selection against large ♂ ♀                          | (a) Viability cost of long development (predation, parasitism, or starvation)<br>(b) Viability cost of fast growth (predation, parasitism, or starvation)<br>(c) Viability cost of reduced agility or increased detectability (size-selective predation or parasitism)<br>(d) Time and energy cost of supporting large size (size-selective starvation)<br>(e) Viability cost of reproduction (due to pleiotropy)<br>(f) Viability cost of heat stress (size-selective mortality)<br>(g) Mutational load |
| 2. Sexual (and reproductive) selection against large ♂                            | (a) Mating or reproductive cost of reduced agility<br>(b) Mating or reproductive cost of energy (and time) limitation  |
| 3. Selection for earlier reproduction at small size in ♀ (reproductive selection) | Energetic cost of reproducing at large size  |
| 4. Selection for earlier reproduction (protandry) in ♂                            | Mating cost when reproducing later at large size   |
| 5. Selection for efficient mate finding that produces dwarf ♂                     | Mating, search, and viability cost when reproducing later at large size  |

at reproduction (Table 1): (1a) To achieve a larger size, it is often assumed that organisms have to grow for longer time; and (1b) If individuals want to achieve a large body size without extending their prereproductive period (i.e., development time), they have to grow faster. In the first case, the longer prereproductive period increases cumulative mortality before reproduction due to predation, parasitism, and/or starvation, given nonzero mortality rates at all times (Roff 1980; Stearns and Koella 1986). In the second case, mortality is likely to increase because of higher predation associated with the riskier foraging necessary to achieve faster growth (Fraser and Gilliam 1992; Werner and Anholt 1993; Abrams et al. 1996), or higher metabolic demands necessary for faster growth under resource limitation (Clutton-Brock et al. 1985; Gotthard et al. 1994; Blanckenhorn 1998). It is obvious that these sources of mortality strongly depend on a variety of environmental variables, particularly temperature, which is known to strongly affect patterns of growth, development, and body size (Atkinson 1994). While there is substantial (and even genetic) evidence for these two trade-offs between development rate and

mortality and between growth rate and mortality (Partridge and Fowler 1993; Arendt 1997), the central problem with relating these viability costs to body size is that individuals which died during juvenile development cannot later be measured (Reznick 1985; Blanckenhorn et al. 1998). It is possible to use propagule, larval, or juvenile size as an estimate of final body size, as all these measures are often positively correlated (Clutton-Brock et al. 1988; Roff 1992: Chapter 10; Sinervo et al. 1992), but this disregards phenotypic plasticity in growth and development, which can often compensate for initial disadvantages in propagule size (Arendt 1997; Nylin and Gotthard 1998). Detection of prereproductive viability selection against large body size based on mechanisms (1a) and (1b) is therefore difficult—perhaps impossible, if due to selective abortion (Trivers and Willard 1973; Clutton-Brock et al. 1985)—except via selection experiments (e.g., Millar and Hickling 1991; Partridge and Fowler 1993; Miyatake 1995).

Greater mortality due to **being** large is expected, based on four further mechanisms (Table 1); these pertain to both adults and juveniles. (1c) Large individuals are more visible

TABLE 2  
Viability selection against large juvenile size

| Species   | Environmental variability | Mechanism           | Method of demonstration                        | References |
|---|---------------------------|---------------------|--|------------|
| <b>MAMMALS</b>  |                           |                     |  |            |
| Humans<br>( <i>Homo sapiens</i> )                     | —                         | ?                   | Stabilizing selection analysis                 | 1          |
| <b>BIRDS</b>  |                           |                     |  |            |
| Great tit<br>( <i>Parus major</i> )                   | +                         | ?                   | Stabilizing selection analysis                 | 2          |
| Blue tit<br>( <i>Parus caeruleus</i> )                | +                         | ?                   | Analysis of field survival                     | 3          |
| Collared flycatcher<br>( <i>Ficedula albicollis</i> ) | +                         | ?                   | Stabilizing and directional selection analysis | 4          |
| <b>REPTILES</b>                                       |                           |                     |  |            |
| Garter snake<br>( <i>Thamnophis sirtalis fitchi</i> ) | +                         | (1c) ?<br>Predation | Stabilizing selection analysis                 | 5          |
| Side-blotched lizard<br>( <i>Uta stansburiana</i> )   | +                         | ?                   | Stabilizing selection analysis                 | 6          |
| <b>AMPHIBIANS</b>                                     |                           |                     |  |            |
| Smooth newt<br>( <i>Triturus vulgaris</i> )           | +                         | ?                   | Stabilizing selection analysis                 | 7          |
| Fire-bellied toad<br>( <i>Bombina orientalis</i> )    | +                         | (1c) ?<br>Predation | Analysis of field survival                     | 8          |
| <b>FISH</b>   |                           |                     |  |            |
| Silverside<br>( <i>Menidia beryllina</i> )            | +                         | (1c)<br>Predation   | Predation experiment                           | 9          |
| Capelin<br>( <i>Mallotus villosus</i> )               | +                         | (1c)<br>Predation   | Predation experiment                           | 10         |
| Trout<br>( <i>Salmo trutta</i> )                      | +                         | (1d) ?              | Analysis of field survival                     | 11         |
| White sucker<br>( <i>Catostomus commersoni</i> )      |                           | (1c)<br>Predation   | Predation experiment                           | 12         |
| False pilchard<br>( <i>Harengula clupeiola</i> )      | +                         | (1c)<br>Predation   | Predation experiment                           | 13         |
| Spot<br>( <i>Leiostomus xanthurus</i> )               | +                         | (1c)<br>Predation   | Predation experiment                           | 14         |

(Continued)

and less agile and maneuverable. This is expected to result in disproportionate predation (Ghiselin 1974; Andersson 1994), and perhaps parasitism (Solbreck et al. 1989; Zuk and Kolluru 1998), on large individuals, despite their greater strength. (1d) Larger individuals require more food to support themselves (and

their offspring), which increases mortality risk under resource limitation (Clutton-Brock et al. 1985, 1988; Reiss 1989; Blanckenhorn et al. 1995; but see Millar and Hickling 1990). This reflects the global argument that, because of competition, there is not enough food in most natural environments to allow individuals to

TABLE 2  
Continued

| Species   | Environmental variability | Mechanism                    | Method of demonstration  | References |
|---|---------------------------|------------------------------|--------------------------|------------|
| INSECTS   |                           |                              |                          |            |
| Melon fly<br>( <i>Bactrocera curcubitae</i> )   |                           | (1a), (1e) ?                 | Selection experiment     | 15         |
| Fruit fly<br>( <i>Drosophila melanogaster</i> ) | +                         | (1b), (1e) ?                 | Selection experiment     | 16         |
| Mosquito<br>( <i>Aedes</i> spp.)                |                           | (1c)<br>Predation            | Predation experiment     | 17         |
| Caddisfly<br>( <i>Chironomus tentans</i> )      | +                         | (1c)<br>Predation            | Predation experiment     | 18         |
| Various aquatic insect larvae                   | +                         | (1c)<br>Predation            | Stomach content analysis | 19         |
| OTHER INVERTEBRATES                             |                           |                              |                          |            |
| Polychaete<br>( <i>Streblospio benedicti</i> )  |                           | (1e) ?                       | Genetic trade-off        | 20         |
| PLANTS  |                           |                              |                          |            |
| <i>Impatiens pallida</i>                        | +                         | (1d) ?<br>Light and moisture | Selection analysis       | 21         |

1) Van Valen and Mellin 1967. 2) Gebhardt-Henrich and van Noordwijk 1991; Linden et al. 1992. 3) Julliard et al. 1996. 4) Linden et al. 1992; Merilä et al. 1997. 5) Jayne and Bennett 1990. 6) Sinervo et al. 1992. 7) Bell 1974, 1978. 8) Kaplan 1992. 9) Gleason and Bengtson 1996. 10) Litvak and Legett 1992; Elliott and Leggett 1997. 11) Elliot 1990a,b. 12) Kelly 1996. 13) Shealer 1998. 14) Rice et al. 1993. 15) Miyatake 1995. 16) Wilkinson 1987; Bierbaum et al. 1989; Partridge and Fowler 1993. 17) Fincke et al. 1997. 18) Macchiusi and Baker 1991. 19) Parker 1993. 20) Levin et al. 1991. 21) Stewart and Schoen 1987.

grow bigger. (1e) Larger individuals in good condition may reproduce earlier in life (because they have grown faster as juveniles) and show greater reproductive effort (Reznick 1985; Madsen and Shine 1994). They are consequently expected to suffer a greater cost of reproduction, which ultimately should become manifested intrinsically as a negative genetic correlation between longevity and early (and high) reproductive effort (Eklund and Bradford 1977; Hillesheim and Stearns 1992; Westendorp and Kirkwood 1998). This is best investigated using selection experiments (Reznick 1985, 1992). (1f) Larger individuals may suffer greater heat stress (discussed under physiological mechanisms below). Mechanisms (1c) and (1d) have been invoked in particular with regard to flying organisms (Andersson and Norberg 1981; Koenig and Albano 1987; Møller et al. 1998), and there is some comparative evidence in birds (Andersson and Norberg 1981;

Balmford et al. 1993; but see below). Some additional (but presumably rare) mechanisms of adult viability selection against large body size are size limitation by the overwintering site (a plant) in a beetle (Ott and Lampo 1991), and the limited availability of large shells in hermit crabs (Vance 1972; Harvey 1990).

Tables 2 and 3 list empirical studies that report (occasional) viability costs associated with large juvenile and adult size, respectively. In some species with continuous growth (particularly fish), size-selective predation is often reported without reference to whether the prey was juvenile or adult, so most studies appear in Table 2 (compare Sogard's (1997) review on size-selective mortality of juvenile fish). The method of demonstration and the (presumed) mechanism are given. Except for some special cases, four classes of studies can be identified. First, experimental studies (e.g., of size-selective predation) are clearly the best,

as they directly investigate a particular mechanism. Second, studies that employ quantitative selection analysis (Arnold and Wade 1984) or some precursor thereof (e.g., Mason 1964) are primarily phenomenological, so the selection mechanism is often unknown or unclear (indicated by question marks in Tables 2–4). Third, studies that analyze survival in the field using a variety of methods are typically correlational, unless manipulations were used. The fourth class is selection or other genetic experiments necessarily restricted to the lab. The environmental variability column in Tables 2 and 3 features a plus sign if the phenomenon has been observed in some environments but not others (i.e., for some traits, with regard to some predators, at some temperatures, in some seasons or habitats), no sign if only one environment or data set was assessed, and a minus sign if the phenomenon was consistent in more than one environment. Juvenile mortality is generally not assessed with regard to sex (Table 2), whereas sex-specific selection for adults is indicated if known (Table 3).

There are few species for which viability selection against large juvenile size has been demonstrated (Table 2), and there are more, but still not many, species for which analogous viability costs of (some aspect of) adult body size have been demonstrated (Table 3). Some patterns with regard to taxonomic group or method emerged. Many studies applied selection analysis and are thus merely phenomenological. Environmental variation is ubiquitous; in a given species, viability selection against large size seems to occur only occasionally. Size-selective predation is common, whereas size-specific parasitism may occur but is rarely (if ever) documented (mechanism (1c): Solbreck et al. 1989; Nishida 1994; Zuk and Kolluru 1998). Energetic costs of supporting large body sizes, mechanism (1d), are often invoked but rarely (if ever) demonstrated (compare physiological mechanisms below). Viability costs of reproduction, mechanism (1e), have been revealed by selection experiments in some taxa, primarily well-studied and common laboratory animals like mice (Eklund and Bradford 1977; Millar and Hickling 1991) or *Drosophila melanogaster* (Wilkinson 1987; Bierbaum et al. 1989; Partridge and Fowler 1993), and it would be desirable to add some more species

to this list (e.g., Miyatake 1995). Few studies of plants were found, but most animal taxa, except the very small bodied and uncommon, are represented. Large-bodied species have the advantage that their mortality can be better observed in the field. On the other hand, experimental (e.g., predation) studies are naturally rare in birds and mammals and more easily conducted with small-bodied species. Interestingly, they are most common in aquatic habitats (Tables 2 and 3).

Research biases, possibly motivated by theory, practical, and/or economic considerations, have certainly contributed to the lack of studies that investigate viability costs of large size. For example, size-selective predation seems to be an issue in aquatic but not terrestrial organisms (Tables 2 and 3). This point is clearly illustrated by the literature of the past ten years (1988–98), which I compiled using the research database OVID. Of 94 studies found on this subject, only 4 involved nonaquatic prey and only 11 nonaquatic predators; 38 studies merely discussed the subject but contained no data, and 9 studies were models. This shows that size-selective predation features prominently in theory. Moreover, in the 47 studies which presented data, predators preferred large individuals of a particular prey species in 27 cases, small individuals in 24 cases, and had no preference in 7 cases; in 11 studies, environmentally-mediated variability in preferences of the predator were reported. This illustrates an additional point. Studies often take the viewpoint of the predator, such as in optimal foraging (e.g., Sutherland 1982; Stephens and Krebs 1986), whereas here we are interested in the viewpoint of the prey. It is likely that several predators prey on the same species, some of which prefer small and others large individuals (e.g., Luning 1992; Rice et al. 1993; Reznick et al. 1996). Therefore, the net result for the prey may be no size-specific mortality differences overall. Studies of interactions of single predator with single prey species are thus a good start but necessarily incomplete. Systematic case studies of prey organisms are needed.

Overall, evidence for viability **benefits** of large size (reviewed in Roff 1992:117; Andersson 1994) is much easier to find than evidence for viability costs. Moreover, the fact that in

TABLE 3  
Viability selection against large adult size

| Species  | Environmental variability; sex affected | Mechanism   | Method of demonstration                                  | References |
|--|---|---|--|------------|
| <b>MAMMALS</b>   |   |   |  |            |
| Reindeer<br>( <i>Rangifer t. tarandus</i> )            | ♀                                       | (1c), (1d) ?  | Life table analysis of field survival                    | 1          |
| Mouse<br>( <i>Mus musculus</i> )                       | ♂ ♀; -                                  | (1b), (1d), (1e)                                      | Selection experiment                                     | 2          |
| Weasel<br>( <i>Mustela erminea</i> )                   | ♂ ♀; +                                  | (1d) ?  | Life table analysis of field survival                    | 3          |
| Kudu<br>( <i>Tragelaphus strepsiceros</i> )            | ♂; +                                    | (1c), (1d)?<br>Predation;<br>Energy limitation        | Life table analysis of field survival                    | 4          |
| Humans<br>( <i>Homo sapiens</i> )                      | ♂ ♀; -                                  | (1b), (1d), (1e) ?                                    | Mortality records  | 5          |
| <b>BIRDS</b>   |   |   |  |            |
| Barn swallow<br>( <i>Hirundo rustica</i> )             | ♂; +                                    | (1c), (1d)<br>Parasitism?;<br>Foraging cost           | Analysis of field survival;<br>Experimental manipulation | 6          |
| Sand martin<br>( <i>Riparia riparia</i> )              | ♂ ♀; +                                  | (1d) ?  | Mortality records  | 7          |
| Herring gull<br>( <i>Larus argentatus</i> )            | ♂ ♀; +                                  | (1d) ?<br>Energy limitation<br>(breeding or winter)   | Stabilizing selection analysis                           | 8          |
| Red-winged blackbird<br>( <i>Agelaius phoeniceus</i> ) | ♂; +                                    | (1d) ?<br>Energy limitation<br>(breeding)             | Analysis of field survival;<br>Experimental manipulation | 9          |
| Brown-headed cowbird<br>( <i>Molothrus ater</i> )      | ♂; +                                    | (1d) ?<br>Energy limitation<br>(winter)               | Analysis of field survival                               | 10         |
| House sparrow<br>( <i>Passer domesticus</i> )          | ♂ ♀; +                                  | (1c); (1d) ?;<br>Storm; Energy<br>limitation (winter) | Directional selection analysis                           | 11         |
| Song sparrow<br>( <i>Melospiza melodia</i> )           | ♂ ♀; +                                  | (1d), (1e) ?  | Directional selection analysis                           | 12         |
| Galapagos finch<br>( <i>Geospiza fortis</i> )          | ♂ ♀; +                                  | (1d)  | Stabilizing selection analysis                           | 13         |
| <b>REPTILES</b>  |   |   |  |            |
| Gecko<br>( <i>Aristelliger praesignis</i> )            | ♂ ♀; +                                  | (1c) ?<br>Predation                                   | Selection analysis                                       | 14         |
| Adder<br>( <i>Vipera berus</i> )                       | ♂ ♀; +                                  | (1d) ?<br>Prey limitation                             | Analysis of field survival                               | 15         |
| Marine Iguana<br>( <i>Amblyrhynchus cristatus</i> )    | ♂ ♀; +                                  | (1d) ?<br>Energy limitation                           | Directional selection analysis                           | 16         |
| <b>AMPHIBIANS</b>                                      |   |   |  |            |
| Bullfrog<br>( <i>Rana catesbeiana</i> )                | ♂; -                                    | (1c)<br>Predation                                     | Analysis of field survival                               | 17         |

(Continued)

TABLE 3  
Continued

| Species   | Environmental<br>variability;<br>sex affected | Mechanism                                      | Method of demonstration                                      | References |
|---|---|--|--|------------|
| FISH  |   |  |  |            |
| Sailfin molly<br>( <i>Poecilia latipinna</i> )      | ♀; +  | (1c)<br>Predation                              | Predation experiment   | 18         |
| Mosquitofish<br>( <i>Gambusia affinis</i> )         | ♀; -  | (1c)<br>Predation                              | Predation experiment   | 19         |
| Pacific salmon<br>( <i>Oncorhynchus nerka</i> )     | ♂ ♀; -  | (1c)<br>Predation                              | Directional selection analysis<br>using fisheries records    | 20         |
| INSECTS   |   |  |  |            |
| Bug<br>( <i>Euschistus variolarius</i> )            | ♂ ♀   | (1c)<br>Storm                                  | Directional selection analysis                               | 21         |
| Bug<br>( <i>Lygaeus equestris</i> )                 | ♀; +  | (1c)<br>Parasitoids                            | Population and sex<br>comparison                             | 22         |
| Bug<br>( <i>Colpula lativentris</i> )               | ♂ ♀; -  | (1c) ?<br>Fungal Parasite                      | Directional selection analysis                               | 23         |
| Spruce bud moth<br>( <i>Zeiraphera canadensis</i> ) | ♀; +  | (1f)   | Laboratory experiment  | 24         |
| White-tailed skimmer<br>( <i>Plathelmis lydia</i> ) | ♂; +  | (1d) ?<br>Energy limitation<br>(breeding)      | Directional selection analysis                               | 25         |
| Damselfly<br>( <i>Enallagma boreale</i> )           | ♀; +  | (1c) ?   | Stabilizing selection analysis;<br>Experimental manipulation | 26         |
| Beetle<br>( <i>Acanthoscellides alboscuteatus</i> ) | ♂ ♀   | Entrapment in<br>overwintering site<br>(plant) | Analysis of field survival                                   | 27         |
| Digger wasp<br>( <i>Bembix rostrata</i> )           | ♀; -  | ?  | Stabilizing selection analysis                               | 28         |
| Parasitoid wasp<br>( <i>Goniozus nephantidis</i> )  | ♀; +  | ?  | Laboratory experiment  | 29         |
| Bee<br>( <i>Centris pallida</i> )                   | ♂   | (1c)<br>Predation                              | Simulated predation exper-<br>iment                          | 30         |
| Burrowing bee<br>( <i>Amegilla dawsoni</i> )        | ♂; -  | (1c), (1d) ?<br>Predation                      | Analysis of field survival                                   | 31         |
| Scorpionfly<br>( <i>Harpobittacus nigriceps</i> )   | ♂ ♀; +  | (1d) ?   | Stabilizing selection analysis                               | 32         |
| Water strider<br>( <i>Aquarius remigis</i> )        | ♂ ♀; +  | (1e) ?   | Directional selection analysis;<br>Experimental manipulation | 33         |
| Fruit fly<br>( <i>Drosophila melanogaster</i> )     | ♀; +  | (1e)   | Selection experiment   | 34         |
| OTHER<br>INVERTEBRATES                              |   |  |  |            |
| Millipede<br>( <i>Alloporus uncinatus</i> )         | ♂ ♀; -  | (1f)   | Laboratory experiment  | 35         |
| Isopod<br>( <i>Asellus aquaticus</i> )              | ♂; -  | ?  | Analysis of field and lab<br>survival                        | 36         |
| Amphipod<br>( <i>Hyalella azteca</i> )              | ♂ ♀; +  | (1c)<br>Predation                              | Stomach content analysis                                     | 37         |

(Continued)

TABLE 3  
Continued

| Species  | Environmental variability; sex affected | Mechanism         | Method of demonstration                                  | References |
|--|---|-------------------|--|------------|
| Waterflea<br>( <i>Daphnia lumholzi</i> )                             | ♂ ♀                                     | (1c)<br>Predation | Stomach content analysis                                 | 38         |
| Waterfleas<br>( <i>Daphnia pulex</i> )<br>( <i>Daphnia hyalina</i> ) | ♂ ♀; +                                  | (1c)<br>Predation | Laboratory predation experiment                          | 39         |
| Copepod<br>( <i>Eudiaptomus gracilis</i> )                           | ♂ ♀                                     | (1c)<br>Predation | Laboratory predation experiment                          | 40         |
| Various Sea urchins  | ♂ ♀; -                                  | (1c)<br>Predation | Stomach content analysis                                 | 41         |
| Various parasitic Gnathid Isopods                                    | ♂ ♀; +                                  | (1c)<br>Predation | Stomach content analysis                                 | 42         |
| MOLLUSKS   |   |                   |  |            |
| Cockles<br>( <i>Cerastoderma edule</i> )                             | ♂ ♀                                     | (1c)<br>Predation | Foraging experiment                                      | 43         |
| Dog-whelk<br>( <i>Nucella lapillus</i> )                             | ♂ ♀; +                                  | ?                 | Stabilizing selection analysis                           | 44         |
| Littleneck clam<br>( <i>Protothaca staminea</i> )                    | ♂ ♀; +                                  | (1c)<br>Predation | Predation experiment                                     | 45         |
| Clam<br>( <i>Anodonta grandis</i> )                                  | ♂ ♀; -                                  | (1c)<br>Predation | Food residue analysis                                    | 46         |
| Oyster<br>( <i>Agerostrea mesenterica</i> )                          | ♂ ♀                                     | ?                 | Stabilizing selection analysis                           | 47         |
| Zebra mussel<br>( <i>Dreissena polymorpha</i> )                      | ♂ ♀; +                                  | (1c)<br>Predation | Stomach content analysis                                 | 48         |
| Marsh periwinkle<br>( <i>Littoraria irrorata</i> )                   | ♂ ♀                                     | (1c)<br>Predation | Predation experiment                                     | 49         |
| Snail<br>( <i>Umbonium vestiarium</i> )                              | ♂ ♀                                     | (1c)<br>Predation | Predation experiment                                     | 50         |
| Snail<br>( <i>Bittum varium</i> )                                    | ♂ ♀                                     | (1c)<br>Predation | Predation experiment                                     | 51         |
| Snail<br>( <i>Cepea hortensis</i> )                                  | ♂ ♀; +                                  | (1f) ?            | Analysis of field survival;<br>Experimental manipulation | 52         |
| Various mollusks   | ♂ ♀; +                                  | (1c)<br>Predation | Analysis of field survival                               | 53         |

1) Skogland 1989. 2) Eklund and Bradford 1977; Millar and Hickling 1989. 3) Powell and King 1997. 4) Owen-Smith 1993. 5) Holzenberger et al. 1991; Westendorp and Kirkwood 1998. 6) Møller et al. 1998. 7) Jones 1987; Bryant and Jones 1995. 8) Monaghan and Metcalfe 1986. 9) Johnson et al. 1981; Searcy and Yasukawa 1981; Yasukawa 1987; Weatherhead and Clark 1994; Rohwer et al. 1996. 10) Johnson et al. 1980. 11) Bumpus 1899; Lowther 1977; Johnston and Fleischer 1981; Lande and Arnold 1983; Crespi and Bookstein 1989. 12) Schluter and Smith 1986. 13) Price 1984; Price et al. 1984; Grant 1986; Gibbs and Grant 1987. 14) Hecht 1952. 15) Forsman 1991a,b, 1993. 16) Wikelski and Trillmich 1997. 17) Howard 1981. 18) Trexler et al. 1994. 19) Britton and Moser 1982. 20) Konovalov and Shevlyakov 1978; Ricker 1981. 21) Lande and Arnold 1983; Crespi and Bookstein 1989. 22) Solbreck et al. 1989. 23) Nishida 1994. 24) Carroll and Quiring 1993. 25) Koenig and Albano 1987. 26) Anholt 1991. 27) Ott and Lampo 1991. 28) Larsson and Tengö 1989. 29) Hardy et al. 1992. 30) Alcock 1995. 31) Alcock 1996. 32) Thornhill 1983. 33) Blanckenhorn et al. 1995; Preziosi and Fairbairn 1996, 1997, 2000. 34) Hillesheim and Stearns 1992. 35) Dangerfield and Chipfunde 1995. 36) Ridley and Thompson 1979. 37) Wellborn 1994. 38) Green 1967. 39) McArdle and Lawton 1979; Scott and Murdoch 1983; Luning 1992; Stibor and Luning 1994. 40) Svensson 1997. 41) Estes and Duggins 1995. 42) Grutter 1997. 43) Sutherland 1982. 44) Berry and Crothers 1968. 45) Peterson 1982; Kabat 1990; Peitso et al. 1994. 46) Hanson et al. 1989. 47) Sambol and Finks 1977. 48) Prejs et al. 1990; MacIsaac 1994; Thorp et al. 1998. 49) Schindler et al. 1994. 50) Berry 1982. 51) Wright et al. 1996. 52) Bantock and Bayley 1973; Knights 1979. 53) Merrick et al. 1992.

TABLE 4  
Sexual selection against large male size

| Species  | Mechanism  | Method of demonstration   | References |
|--|--|---|------------|
| <b>BIRDS</b>   |  |   |            |
| Sharp-tailed grouse<br>( <i>Tympanuchus phasianellus</i> ) | (2b) ?<br>Courtship energetics                         | Directional selection on mating success and courtship characteristics     | 1          |
| Moorhen<br>( <i>Gallinula chloropus</i> )                  | (2b) ?<br>Incubation energetics<br>(sex role reversal) | Negative relationship with mating success                                 | 2          |
| Dunlin<br>( <i>Calidris alpina</i> )                       | (2a), (2b)<br>Courtship display                        | Negative relationship with courtship characteristics                      | 3          |
| Tengmalm's owl<br>( <i>Aegolius funereus</i> )             | (2b)<br>Food provisioning energetics                   | Negative relationship with provisioning rate and breeding success         | 4          |
| Kestrel<br>( <i>Falco tinnunculus</i> )                    | (2b)<br>Food provisioning energetics                   | Negative relationship with provisioning rate and mate choice (experiment) | 5          |
| Pied flycatcher<br>( <i>Ficedula hypoleuca</i> )           | ?  | Stabilizing selection on mating success                                   | 6          |
| <b>FISH</b>  |  |   |            |
| Coho salmon<br>( <i>Oncorhynchus kisutch</i> )             | (2a)<br>Sneak strategy                                 | Disruptive selection on mating success                                    | 7          |
| Mosquitofish<br>( <i>Gambusia holbrooki</i> )              | (2a)<br>Sneak strategy                                 | Negative relationship with insemination success                           | 8          |

(Continued)

some well-studied species body size is sometimes found to confer a viability advantage and sometimes a disadvantage (e.g., red-winged blackbirds: Yasukawa 1987; Langston et al. 1990; Weatherhead and Clark 1994; Rohwer et al. 1996) implies spatio-temporal, sex, and life-stage specific variability in viability selection, and generally calls for investigating any selection mechanism in multiple environments. All this is not surprising. Large body size is highly correlated with (i.e., either the cause or the consequence of) good condition, and individuals in good condition are bound to survive better (Zeh and Zeh 1988; Andersson 1994). Therefore, good condition due to good nutrition often masks expected viability costs of large size (van Noordwijk and de Jong 1986; Alatalo et al. 1990; Schluter et al. 1991). It is thus important to account for variation in (physiological) condition when assessing the fitness consequences of body size.

#### SEXUAL SELECTION AGAINST LARGE BODY SIZE

Several other mechanisms have been proposed to select for small body size in either sex (Table 1). Except for sexual selection favoring small males, direct empirical evidence for these mechanisms is poor.

Despite overwhelming evidence for sexual selection for large male size, sexual selection for small male size also occurs in nature (Ghiselin 1974; Andersson 1994). Both processes may actually occur in the same species (e.g., sailfin molly: Travis 1994; water striders: Blanckenhorn et al. 1995), resulting in stabilizing sexual selection (Mason 1964; Moore 1990). The mechanisms invoked are analogous to mechanisms (1c) and (1d) given above for adult mortality (Table 1). (2a) Smaller males may be more agile and maneuverable when courting, searching for mates, defending mating territories, and foraging to provision their offspring; this results in increased mating and reproduc-



TABLE 4  
Continued

| Species   | Mechanism                   | Method of demonstration  | References |
|---|-----------------------------|--|------------|
| INSECTS   |                             |  |            |
| Wasp<br>( <i>Trypoxylon politum</i> )                     | ?                           | Stabilizing selection on mating success                          | 9          |
| Damselfly<br>( <i>Enallagma hageni</i> )                  | (2a) ?<br>Courtship display | Stabilizing selection on mating success                          | 10         |
| Damselfly<br>( <i>Coenagrion puella</i> )                 | (2a) ?<br>Courtship display | Negative relationship with mating rate                           | 11         |
| Pond dragonfly<br>( <i>Libellula luctuosa</i> )           | (2a) ?<br>Courtship display | Stabilizing selection analysis                                   | 12         |
| Damselfly<br>( <i>Enallagma boreale</i> )                 | (2a) ?<br>Courtship display | Stabilizing selection on mating success                          | 13         |
| California Oak Moth<br>( <i>Phryganidia californica</i> ) | ?                           | Stabilizing selection on mating success                          | 14         |
| Butterfly<br>( <i>Heliconius sara</i> )                   | (2a) (2b) ?                 | Negative relationship with territorial success                   | 15         |
| Fruitfly<br>( <i>Drosophila subobscura</i> )              | (2a)                        | Negative relationship with courtship success                     | 16         |
| Fruitfly<br>( <i>Drosophila montana</i> )                 | (2a) ?                      | Disruptive selection on mating success                           | 17         |
| Fruitfly<br>( <i>Drosophila silvestris</i> )              | (2a)<br>Courtship display   | Negative relationship with courtship success                     | 18         |
| Midge<br>( <i>Chironomus plumosus</i> )                   | (2a) ?<br>Flight agility    | Negative relationship with mating success                        | 19         |
| Beetle<br>( <i>Tetraopes tetraophthalmus</i> )            | ?                           | Stabilizing selection on mating success                          | 20         |
| Water strider<br>( <i>Aquarius remigis</i> )              | (2b)<br>Energy limitation   | Experimentally induced negative relationship with mating success | 21         |

1) Gratson 1993. 2) Petrie 1983. 3) Blomqvist et al. 1997. 4) Hakkarainen and Korpimäki 1991, 1995. 5) Hakkarainen et al. 1996. 6) Alatalo and Lundberg 1986. 7) Gross 1985; Fleming and Gross 1994. 8) Bisazza and Pilastro 1997; Pilastro et al. 1997. 9) Molumby 1997. 10) Fincke 1982. 11) Banks and Thompson 1985. 12) Moore 1990. 13) Anholt 1991. 14) Mason 1969. 15) Hernández and Benson 1998. 16) Steele and Partridge 1988. 17) Aspi and Hoikkala 1995. 18) Boake 1989. 19) Neems et al. 1990, 1992, 1998. 20) Mason 1964; Scheiring 1977; McCauley 1982. 21) Blanckenhorn et al. 1995.

tive success (Banks and Thompson 1985; Steele and Partridge 1988; Blomqvist et al. 1997; Neems et al. 1998). (2b) Smaller individuals require less food to support themselves, so smaller males should have free energy and time for any activity that increases their mating and reproductive success; such activities include the pursuit of mates, courtship and brood provisioning, or investment in their sperm supply, particularly in species with sexual scramble competition (Ghiselin 1974; Schwagmeyer 1988; Jönsson and Alerstam 1990; Andersson 1994; Taborsky 1998; Simmons et

al. 1999). I call this the small male time-budget advantage (Blanckenhorn et al. 1995). (Some people may debate whether to call this sexual selection at all, but this is a matter of semantics and besides the point here.)

I found evidence in the literature for sexual selection favoring small males in 21 species, spatio-temporal variation in this phenomenon again being common (e.g., *Tetraopes tetraophthalmus*: Mason 1964; Scheiring 1977; McCauley 1982; *Drosophila montana*: Aspi and Hoikkala 1995; Table 4). Studies either showed direc-

tional or disruptive selection favoring small males or stabilizing selection favoring intermediate males, mating advantages of small males, or advantages of small males in behavior ultimately relating to mate acquisition or offspring care. Evidence comes primarily from flying organisms. Interestingly, evidence for agility disadvantages of large size (2a) comes primarily from insects, particularly odonates, whereas evidence for energetic disadvantages of large size (2b) comes primarily from birds (Table 4). This likely has to do with the fact that the former mate on the wing whereas the latter do not. In selection studies, however, mechanism (2a) is often invoked but no direct behavioral evidence is generally presented. Conversely, some behavioral studies demonstrate advantages of small males in courtship but do not investigate mating success or sexual selection in the wild (e.g., Steele and Partridge 1988). In general, an integrative approach that includes experiments in multiple environments is needed to fully investigate the mechanisms and consequences of sexual selection against large body size. The fact that at least three studies found support for this mechanism only at food-limited conditions is reassuring (Hakkarainen and Korpimäki 1991, 1995; Blanckenhorn et al. 1995; Hakkarainen et al. 1996).

Species for which alternative (e.g., sneak) mating strategies or tactics have been documented, sometimes involving sperm competition (e.g., Wikelski and Bäumler 1996; Simmons et al. 1999), might be added to Table 4 (reviewed by Taborsky 1994, 1998; Gross 1996). However, I only included those studies where the smallest males have been shown to have greater mating or reproductive success than at least medium-sized males; that is, when there is directional or disruptive selection on male size (Gross 1985, 1996; Fleming and Gross 1994; Pilastro et al. 1997). This is the rare case. Alternative mating systems are often assumed to be maintained by negative frequency-dependent selection, implying roughly equal mating success of all morphs or body sizes on average, but this is very difficult to show (reviewed by Austad 1984; Gross 1996; e.g., Gross 1991; Shuster and Wade 1991; Ryan et al. 1992). Most often, small males exhibit best-of-a-bad-job strategies or tactics which augment their mating success to some extent

but not quite to the level of larger males (Dawkins 1980). In the latter two cases, the behavioral mechanism, but not necessarily small body size, may be favored by selection unless both are genetically coupled. Most of the examples of alternative mating systems reported in fish and some other species are likely to fall into this category (see Dominey 1980, 1984; Gross and Charnov 1980; Farr et al. 1986; Zinner and Kallman 1989; Shuster and Wade 1991; Taborsky 1994, 1998; Gross 1996; Wikelski and Bäumler 1996; Alcock 1997a; Bisazza and Pilastro 1997; Simmons et al. 1999). By the same reasoning, patterns of assortative mating by size do not necessarily indicate sexual selection favoring small males. Loading constraints may prevent small males from carrying large females, but not large males from carrying small females (Adams and Greenwood 1987). Similarly, the requirement of a (mechanical) size match in pairs of the fish *Xenotoca eiseni*, if anything, may indicate equal mating success of fish of various sizes and thus no sexual selection on body size (Bisazza 1997; Pilastro et al. 1997).

#### OTHER DISADVANTAGES OF LARGE BODY SIZE

Some authors have focused on selection for smaller female size (rather than selection for larger male size) when attempting to explain male-biased SSD in mammals and birds (reproductive selection: Table 1, mechanism (3); Downhower 1976; Erlinge 1979; Willner and Martin 1985; Andersson 1994). Fecundity generally increases with size and may reach an asymptote at large body sizes (e.g., Madsen and Shine 1994; Blanckenhorn et al. 1999), but fecundity selection favoring small female size has not been invoked or found. An alternative argument is again based on energetics: smaller individuals need less energy and can thus reproduce sooner, which supposedly confers a fitness advantage, especially in seasonal habitats that allow only one (or few) breeding attempts per year. This advantage is particularly great in females, as they invest much more in reproduction than males. To test this plausible hypothesis *within* a species, it needs to be shown that small females indeed breed earlier and that this confers greater reproductive success. To my knowledge, empirical evidence of this sort is absent. One study in red-winged blackbirds

that specifically tested this prediction found the opposite: large females bred earlier (Langston et al. 1990). This is not surprising, for the same reason as given above with regard to mortality: small females may be in bad condition and therefore breed later. Furthermore, life-history theory suggests that earlier reproduction confers a fitness advantage only (in times) when populations are increasing (Charlesworth 1980; Lande 1982).

Energetic comparisons **between** the sexes (Erlinge 1979; Sandell 1989) are but of limited help in addressing this hypothesis because sex-specific metabolic efficiency and growth rates may be the consequence, rather than the cause, of particular patterns in body size dimorphism, and may relate to traits other than body size (e.g., behavior). In principle this also holds true for comparisons of mortality patterns between the sexes (Clutton-Brock et al. 1985; Promislow 1992). However, the equilibrium view of SSD indeed predicts stronger viability counterselection in males than in females (i.e., male-biased mortality) if sexual selection is stronger than fecundity selection (Figure 1; Clutton-Brock et al. 1985), but this should also be detectable as greater mortality of larger male juveniles (cf. discussion of mechanisms (1a) and (1b) above). Nonetheless, several authors appear to be satisfied with comparative evidence and argue, particularly for mammals, that differential optimization of energy allocation to growth and reproduction is the primary evolutionary force that produces life span, mortality, and consequently body size differences between the sexes and different species (Clutton-Brock et al. 1982, 1985; Promislow 1992; Charnov 1993: Chapter 5; Kozlowski and Weiner 1997).

By a similar mechanism, selection may favor early reproduction in males (protandry: Table 1, mechanism (4); Wiklund and Fagerström 1977; Travis 1994; Zonneveld 1996). In species where encounter rates with mates are low and individuals reproduce seasonally for only a short period, males may gain an advantage by entering the mating pool early. To emerge early, males are assumed to abbreviate their development at the expense of a reduction in size (cf. mechanism (1a); Roff 1980). While there is **indirect** evidence from comparative studies across species and comparisons between the sexes that support this selection mechanism

(Wiklund and Forsberg 1991), empirical studies within species often find that males can emerge early **and** be large, due to better condition and/or adaptive increases in growth rate (Nylin et al. 1993; Blanckenhorn 1998; Nylin and Gotthard 1998). Just as for females, it therefore needs to be shown that small males emerge earlier and that this confers higher fitness; one without the other is insufficient (e.g., Alcock 1997b). **Direct** empirical support for this hypothesis is also lacking.

Lastly, there are extreme cases of species with so-called dwarf males that are very much smaller than the female, such as anglerfish or spiders (Table 1, mechanism (5); Andersson 1994:255). To explain this phenomenon, several of the previous arguments have been invoked in conjunction. If the chance for a male to mate at all is very small, it does not pay to grow very large. Instead, a male should mature fast to increase his chances to reach reproduction and find a mate (Vollrath and Parker 1992). To ensure fertilization of at least one batch of eggs, the resulting dwarf males can then permanently attach to a large female (Ghiselin 1974), be extremely mobile due to their agility advantage ("roving males": Ghiselin 1974; Vollrath and Parker 1992), or perhaps better avoid sexual cannibalism by the female (Elgar 1991). Comparative evidence supports some of these mechanisms in spiders, but such evidence is merely correlational (Elgar 1991; Vollrath and Parker 1992; but see Prenter et al. 1998). Direct empirical evidence that shows that small, roving males have higher reproductive success is still lacking (to the contrary: see e.g., Vollrath 1980).

#### PHYSIOLOGICAL MECHANISMS

Several of the selection mechanisms against large body size listed in Table 1 are ultimately grounded in physiology. Physiological allometries are well established and represented in the literature (Peters 1983; Calder 1984; Schmidt-Nielsen 1984; Reiss 1989). Mechanisms (1d), (2b), and (3) are based on the fact that metabolic rate (i.e., energy dissipation) scales differently with body mass than processes that affect energy assimilation, such as locomotion, rendering it increasingly prohibitive to support heavier bodies in everlimiting environments. Foraging, courting, and any other energetically expensive activity that affect individual fitness

should therefore become ever more time and energy consuming for larger individuals. While this argument is physiologically sound and investigated primarily in small flying organisms with extreme energy demands like moths, hummingbirds, or bats (Voigt and Winter 1999 and references therein; but see Millar and Hickling 1990), these mechanisms should ultimately result in greater mortality or reduced reproductive success of large individuals at the ecological level; it is this level of biological organization at which evidence for these mechanisms is scant. Note that mechanism (1d) in Table 3 bears a question mark in most cases as it is often supposed but rarely shown. Mortality costs relating to energy limitation may be difficult to detect in the field but can be experimentally addressed (e.g., Blanckenhorn et al. 1995). One strong experimental test would be to keep (or select) organisms at high density and/or low food supply over several generations, with the appropriate low density/high food supply control. This should result in the evolution of (genetically) smaller body sizes. To separate the effects of food on growth and development during the juvenile stage from those on maintenance at the adult stage, the treatment should be delivered separately to juveniles and adults.

A second physiological argument invoked in limiting body size is that larger organisms may have increased difficulties dissipating heat at high temperatures (mechanism (1f) in Table 1). Heat loss in cold climates is reduced by a relatively small body surface (Bergmann's rule: see Atkinson 1994); i.e., a large body with short appendages. Conversely, it is increased in warm climates by a relatively large body surface; i.e., a small body with relatively long appendages. Comparative evidence for the latter so-called Allen's rule is mixed at best (for some recent studies in birds with conflicting results see McGillivray 1989; Wiedenfeld 1991; Rasmussen 1994; Whaley and White 1994; Bried and Jouventin 1997). For endothermic animals like birds and mammals, larger bodies may actually be advantageous in hot climates (Weathers 1981; Schmidt-Nielsen 1997:271). On the other hand, Furuyama and Ohara (1993) found a correlated reduction in body size when selecting for increased heat tolerance in rats. Larger ectothermic animals, in contrast, typically feature

higher body temperatures, so the argument may hold (e.g., Coelho 1991; Seebacher et al. 1999); it has even been invoked to explain the extinction of dinosaurs (Schmidt-Nielsen 1984; Seebacher et al. 1999). I found only two studies that show that large individuals of a given species suffer increased mortality due to heat stress, however (Carroll and Quiring 1993; Dangerfield and Chipfunde 1995; Table 3).

#### EVOLUTIONARY MECHANISMS

In addition to the preceding ecological and physiological arguments, there are evolutionary arguments about what keeps organisms small. As shall be seen, these types of arguments do not differ in principle but merely differ in the level of biological organization at which they are expressed (process vs. pattern).

Selection for large body size may eventually be balanced not by selection but by deleterious mutations that accumulate in the genome (mutation-selection balance; Barton and Turelli 1989; Wayne and Mackay 1998). This mechanism is listed as (1g) in Table 1. Of course, these mutations must eventually affect some measurable fitness component at the ecological level, such as viability or hatching success. But that mortality is intrinsic rather than extrinsic (i.e., caused by selection). The same reasoning applies if selection for large size is constrained (and thus counteracted) by negative genetic correlations among fitness components due to pleiotropy or genotype-environment interactions (Barton and Turelli 1989; Roff 1997; Wayne and Mackay 1998). Intrinsic sources of mortality are best investigated using artificial selection, but one recent test of the mutation-selection balance hypothesis in *Drosophila melanogaster* found no evidence with regard to body size (Wayne and Mackay 1998).

Cope's rules state that: (1) taxa evolve to larger body size over evolutionary time, and (2) that larger organisms and taxa are more likely to go extinct (McLain 1993). They merely describe patterns without reference to specific processes (and are therefore not listed in Table 1). While these rules were conceived with large fossil mammal species in mind, they can be generalized to apply to any large-bodied lineages within a given taxon (McLain 1993). Contrary to popular belief, evidence for the

first rule in fossil species appears to be little more than anecdotal (Gould 1997; Jablonski 1997). Cope's second rule can actually be tested even with extant species, particularly as it relates to the current interest in conservation biology in estimating extinction rates of populations of rare plants and animals (e.g., Hughes et al. 1997). Within each taxon, this rule predicts that larger species should occur in smaller populations that are more likely to go extinct. Siemann et al.'s (1996) data on insects may be construed to support this contention, but I am not aware of any other such evidence.

#### CONCLUSIONS

Schluter et al. (1991) concluded that there is more evidence for opposing selection on traits than for its lack (see also Travis 1989). Body size is probably the character most often invoked as affecting individual fitness of organisms. Almost ten years later, I must conclude that empirical evidence for selection and other processes that limit body size in natural populations lags far behind the vast increase in sexual selection studies that demonstrate the advantages of large body size (Andersson 1994). I have argued that difficulties in demonstrating selection against large body size at the individual organismic level is one major reason for this lack.

Research efforts should therefore focus specifically on the several costs of being large, as outlined in Table 1. Because it is likely that counterbalancing selection on body size occurs only occasionally in time and space, only at some life stages and not others, and perhaps only in one sex and not the other (Grant 1986; Travis 1994; Reeve and Fairbairn 1996; Wikelski and Trillmich 1997), and because body size is frequently confounded by condition, experimental approaches in multiple environments are necessary. We need more comprehensive case studies of particular model species, as few

encompassing data sets on the advantages and disadvantages of large size exist in any species to date. Estimates of lifetime reproductive success are most desirable (Charlesworth 1980; see Clutton-Brock 1988 for examples). As these are difficult to obtain, studies of the same species that focus on the various fitness components (i.e., fecundity, viability, or mating success) need to be integrated (e.g., Arak 1988), using life-history simulations if necessary (e.g., Madsen and Shine 1994). Theoretical studies can further help elucidate whether sporadic selection in time and space is sufficient to counterbalance perpetual and strong selection for large body size. Plausible physiological hypotheses are often investigated mechanistically, or by comparative studies, but rarely in terms of fitness consequences at the individual level. This should be corrected. Genetic studies are difficult, laborious, and largely restricted to organisms which can be easily kept in the laboratory, but are necessary for revealing possible intrinsic fitness costs of large size. Lastly, research and publication biases can restrict the scope of investigation and should therefore be overcome.

In contrast, comparisons among species or the sexes are helpful to detect patterns and generate hypotheses but are limited in that they are correlational, possibly confound cause and effect, and cannot investigate the actual mechanisms involved (e.g., Andersson and Norberg 1981; Clutton-Brock et al. 1985; Sandell 1989; Promislow 1992; Balmford et al. 1993). The albeit weak empirical and experimental evidence compiled here that shows the disadvantages of large body size testifies that they can, and should, be demonstrated, given some effort.

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